Northern Territory Naturalist (2010) 22: 31-44

Fine-scale patchiness of burns in a mesic eucalypt savanna differs with fire season and Sorghum abundance

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Abstract

Canopy tree populations in the eucalypt savannas of northern Australia consistently show bottlenecks in the transition of young trees to the canopy layer. This is most likely due to frequent fires, where young trees are caught in a "fire trap", suffer topkill and regenerate from underground tissues year after year. Little is known of fire behaviour at the spatial scale of individual juvenile trees. This paper presents field measurements of small-scale, 10 cm (microsite), burn patterns and patch sizes following set fires in the early dry season, late dry season, and wet season. Fire treatments were repeated in plots dominated by a native annual grass (Sorghum) and in others with little or none of this grass. Both late dry season and wet season fires left few or no microsites unburnt, regardless of understorey type. With early dry season fire, however, understorey type made a difference: 47% of the microsites were left unburnt in plots with little or no Sorghum compared to only 5% in Sorghum-dominated plots. Further, the early dry season fire pattern was very patchy, resulting in both large and small areas of burnt vegetation. In Sorghum-dominated plots, more than half the patches were ≥ 10 m in size and only a third were < 3 m in size, whereas in plots with little or no Sorghum, 99% of burnt patches were < 10 m in size, and 41% were < 0.5 m in size. Thus, only a regime of early dry season fire with little or no Sorghum in the understorey creates potential "windows of escape" for juvenile trees. The study has implications for management of savanna trees by fire.

Introduction

A common finding in studies of canopy tree populations in the eucalypt dominated savannas of northern Australia is a demographic bottleneck in the transition of juvenile and sapling trees to the canopy layer (Werner 1986; Russell-Smith *et al.* 2003a; Werner *et al.* 2006; Lehmann *et al.* 2009; Williams 2009; Prior *et al.* 2010). Although more than one factor may be responsible for the bottlenecks, fire is most likely the main cause. Frequent fires repeatedly kill the above-ground stems and leaves of young trees which have to be rebuilt from persistent underground tissues. In effect the young trees are caught year after year in a "fire trap" (Hoffmann *et al.* 2009), forming a pool of juvenile trees with their own population dynamics of "births" and "deaths" (Werner *et al.* 2006).

"Escape" of young trees from fire is critical for transition to canopy size in the northern savannas. If frequent fires are patchy at ground level, a juvenile tree might be able to escape being burnt altogether, and if this occurs repeatedly, over time it would be able to attain the height of the canopy layer where it could withstand all but the most intense fires. Although much is known about fire behaviour and patch sizes at the Landsat pixel size (30 m or more) (e.g. Russell-Smith *et al.* 1997), very little is known about fire behaviour or unburnt patches of vegetation at the spatial scale of individual juvenile trees (e.g., at 10 cm scale). Indeed, very little is understood in any of the world's savannas about the type and frequency of fires, and/or other factors such as rainfall, herbivory or understorey type, that permit or enhance the transition of a young tree to canopy size (see Midgley *et al.* 2010).

Although the seasonal timing of fire is known to affect survival and growth of established adult trees (Lonsdale & Braithwaite 1991; Williams *et al.* 1999; Werner 2005; Prior *et al.* 2006; Lehmann *et al.* 2009; Murphy *et al.* 2010), much less is known about the differential effect on juvenile trees, which ideally should include information about fire behaviour at the spatial scale of individual juveniles. Further, although total understorey biomass (Werner *et al.* 2006) and understorey type (Werner & Franklin in press) are known to affect survival of juvenile trees, potential differences in fire behaviour between grass and non-grass understoreys has not been reported previously.

Here, field measurements are presented of the fine scale pattern of ground-level burns by fires set in three different seasons (early dry, late dry, and wet) in two types of native understorey vegetation (high abundance of a common dominant annual grass, and little to none of this grass but a cover consisting mainly of perennial herbs).

Methods

Background: fire seasons and understorey types

Three major types of fires are commonly identified in the Top End of the Northern Territory, described relative to the very strong annual cycle of precipitation where 84% of 1,290-1,580 mm precipitation falls from December to March (Gill *et al.* 1987, 1996; Finlayson & von Oertzen 1996; Russell-Smith *et al.* 1997, 2003b; Williams *et al.* 1998; Andersen *et al.* 2003; Russell-Smith & Edwards 2006). The seasons are defined relative to recent weather, rather than calendar months, and thus vary in start and duration from year to year (Taylor & Tulloch 1985):

- early dry season: generally slow-moving, trunk-scorching, ground fires of low intensity; almost entirely set by humans, both historically by Aboriginal peoples and today by a wide range of land managers;
- late dry season: generally rapid-moving, canopy-scorching fires of high intensity as a consequence of greater leaf litter, drier fuels and more severe fire weather; mainly human set, but also caused by lightning; and
- early wet season: generally rapidly-moving, usually high-intensity fires, but may be lower intensity than late dry season fires depending on fuel, weather and the amount of recent rainfall. These fires are rare, sometimes started by lightning but more often by humans for management purposes.

As in many savannas, almost all fires are ground (not canopy) fires, but some may attain high intensities depending on the amount, type, and moisture content of grassy fuel. Large fuel loads (1-6 tonnes ha^{-1}: Cook *et al.* 1998; Williams *et al.* 1998, 1999; Bowman *et al.* 2007) are a consequence of the strongly seasonal rainfall and the subsequent drying of understorey plants. The main grassy component of fuel is a species of native annual sorghum, *Sorghum brachypodum* Lazarides (formerly *Sorghum intrans* F. Muell. and *Sarga intrans* (F. Muell.) Spangler) (Lazarides *et al.* 1991; Spangler 2003), commonly called Spear Grass or simply "Annual Sorghum". These grasses have single stems, often more than 2 m height; they set seed and die back at the end of the wet season, before almost all other native grasses and herbaceous forbs, and crumple into a perched, aerated, and easily ignited fuel by the time early dry season fires begin (Andrew & Mott 1983; Andrew 1986; Williams *et al.* 2003). In the absence of Sorghum (or introduced African grasses), the understorey is a mixture of smaller annual grasses, perennial grasses, forbs with rosettes and/or single to a few branching stems, and a scattering of small woody stems of trees and shrubs. All these plants delay browning off, or senescing, until the middle or late dry season (Williams *et al.* 2003).

Study area

The study was conducted in Kakadu National Park (KNP), specifically at the Kapalga Research Station (12°34'S, 132°22'E). The geomorphology, soils, climate, and vegetation of the Kakadu region are detailed by Taylor & Dunlop (1985), Press *et al.* (1995) and Finlayson & von Oertzen (1996), and those of Kapalga by Andersen *et al.* (2003).

The study was conducted in 1988 and 1989 in the southern half of Kapalga, where feral water buffalo had been excluded for six years after a period of heavy grazing for some 30 years prior to their removal. In September 1987, a high-intensity fire had burnt all study sites, so little previous-year litter remained in 1988. All study sites had similar woody canopy cover and size structure of mature trees. This study pre-dated, and was not part of, the Kapalga fire experiment (Andersen *et al.* 2003).

Both early dry season and late dry season fire treatments were set up in Compartment J (see map of Kapalga in Andersen *et al.* 1998), approximately 20 km^2 in size. For the early dry season fire treatments, eight different plots, each 30 x 30 m (total area 7,200 m^2) were mapped. Four were dominated by Sorghum (40-80% ground cover) (hereafter "Sorghum plots") and four had between 0 and 20% ground cover of Sorghum (hereafter "plots with little or no Sorghum"). Similarly, the late dry season fire treatment consisted of eight different plots, each 30 x 30 m (total area 7,200 m^2), four with Sorghum and four with little or no Sorghum.

For wet season fire treatments, ten plots, each 20 x 50 m (total area 10,000 m^2) were established, six dominated by Sorghum and four with little or no Sorghum. The plots were located adjacent to Compartments E, F, G, H, L, and P (see Andersen *et al.* 1998).

For the unburnt comparisons, eight plots, each 20 x 50 m (total area 8,000 m^2), were set up, half in Compartment C with ground cover dominated by Sorghum and half in Compartment S with little or no Sorghum.

For all fire treatments, care was taken to pair the Sorghum and little or no Sorghum plots wherever possible, and pairs were sited across the perceived gradual topographic gradient so that any differences would not be attributable to location on the gentle slope.

Understorey vegetation

The projective ground cover (%) of herbaceous species and woody stems < 2 m height was recorded in each of the 34 study plots in the early dry season of 1988 prior to the first fire treatment, using 20 one-metre square subplots within each plot (five randomly placed subplots along four 30-metre transects). Further, more than 3,000 juvenile trees were individually marked and monitored for three years (Werner & Franklin in press).

Prescribed fires

The wet season, early dry season, and late dry season fires were lit in late December 1988, late May 1989, and late September 1989, respectively. Fires were set using drip cans and multiple ignition sites across a transect, upslope of relevant compartment sections, on a day with little wind. They were set more than 100 m away from the plots so that whereas the fires were set as "fronting" fires, they behaved in a more realistic, natural landscape pattern by the time they arrived at the monitored plots. After the fires, the heights of charring (dark discolouration of bark) and scorching (withering of leaves due to heat) and ground-level patchiness of the fires were assessed along four 30 m transects within each plot. The fires were judged to be "low intensity" or "high intensity" based on the occurrence and height of scorching and charring (Gill *et al.* 1987; Williams *et al.* 1998, 1999).

Patchiness of burns

Within one month of each fire, a fine-scale, ground-level assessment of the area burnt was made. Along the upslope boundary (or eastern boundary if there was no discernible slope) of each 30 m study plot, four transects (at the 6 m, 12 m, 18 m, and 24 m location) were run across the plot to the opposite side. Along each transect, the distance along the ground of "burnt" or "unburnt" vegetation was recorded to the nearest 10 cm. Where a burnt patch intersected one plot boundary, only the width of the patch within the plot was recorded. In some cases the burnt patch intersected both ends of the 30 m plot boundary, in which case the patch size was recorded as > 30 m.

A chi-square test was used to examine differences in burn patchiness between Sorghum and little or no Sorghum plots after early dry season fire. The number of degrees of freedom was calculated as (6 patch sizes –1) (2 grass types –1) = 5. No further analysis was conducted on fires set at other seasons as nearly all ground was burnt regardless of understorey type.

Total area burnt by patch size

Extrapolation of patch size frequencies to the total area of various size patches per hectare was performed for early dry season fires only, using the linear measurements of patch sizes, calculating area (assuming a circle) of each patch, and standardizing the sums to one hectare (10,000 m^2). These calculations are estimates of further differences between Sorghum and little or no Sorghum plots.

Results

Pre-fire understorey composition

All plant species were natives; there were no exotic plants in the study plots (Table 1). In Sorghum plots, Annual Sorghum was by far the most abundant species, 40-80% projected ground cover (mean = 70%), compared to plots with 0-20% (mean = 7%) cover of Sorghum. Further, total ground cover was generally higher in Sorghum plots (50-85 % total cover) compared to plots with little or no Sorghum (30-65% total cover). Conversely, ground cover of herbaceous dicotyledons tended to be less in Sorghum plots than plots with little or no Sorghum (< 10% and > 20% per plot, respectively). The ground cover of the main forb species, (herbaceous dicotyledons with single or multi-stems and/or basal rosettes, eg, *Mitrasacme* spp., *Stylidium* spp., and *Spermacoce* spp.) tended to be relatively greater in plots with little or no Sorghum than in Sorghum plots (all species collectively, means = 22% vs. 15%, respectively) (Table 1).

Fire intensity and total area burnt

Early dry season fires were of low-intensity with char heights < 2 m, and scorch heights < 3.5 m; the canopy leaves of the tallest trees were not scorched. The late dry season and wet season fires were both of high intensity. These fires charred tree trunks at heights 2-7 m above ground level and scorched and/or burnt the leaf canopy.

With early dry season fires, grass abundance affected the percentage of 10 cm microsites burnt. In stands with little or no Sorghum, only 53% of the microsites were burnt compared to nearly all (95%) microsites in Sorghum plots (Figure 1). In late dry season fire plots, literally all of the ground surface area was burned, regardless of grass abundance, so essentially all juvenile trees experienced fire. Similarly, grass abundance made little difference in the wet season fire plots, where 99% and 93% of the microsites experienced fire in Sorghum vs. little or no Sorghum plots, respectively (Figure 1).

Table 1. Understorey vegetation, as percentage projective ground cover, summarized across all plots with high abundance of Sorghum vs. little or no Sorghum, at the end of growing season (May) prior to the setting of fires. The individual species named were frequent and appeared in at least half of the plots. All species are natives; there were no exotic plants in the study plots.

Species or group	Habit	Sorghum plots	Little or no Sorghum plots
Sorghum brachypodum Lazarides & other sorghums	Annual grass	40-80% (mean = 70%)	0-20% (mean = 7%)
Pseudopogonatherum contortum (Brongn.) A. Camus	Annual grass	7%	9%
Other annual grasses (collectively)*	Annual grass	4%	2%
Alloteropsis semialata (R. Br.) Hitchc.	Perennial grass	5%	9%
Heteropogon triticeus (R. Br.) Stapf. and *H. contortus* (L.) P. Beauv. ex Roem. & Schult.	Perennial grass	8%	5%
Chrysopogon latifolius S. T. Blake and *C.* fallax S. T. Blake	Perennial grass	3%	< 1%
Other perennial grasses (collectively)**	Perennial grass	< 1%	< 1%
Dicotyledonous herbs (collectively) (basal rosettes, single or multi-stemmed)***	Annual and perennial forbs	15%	22%
Woody stems; shrubs and trees < 2 m height (collectively)	Perennial woody plants	10%	10%
Overall vegetation percentage cover		**50-85%**	**30-65%**

* Other annual grasses include *Panicum mindanaense* Merr., *Setaria apiculata* (Schribn. & Merr.) K. Schum., and *Thaumastochloa major* S. T. Blake, among others. ** Other perennial grasses include *Mnesithea rottboelhoides* (R. Br.) de Konig & Sosef., among others. *** Dicotyledonous forbs include species of *Stylidium* (Stylidiaceae), *Mitrasacme* (Loganiaceae), and *Spermacoce* (formerly *Borreria*) (Rubiaceae), among others.

Patchiness

Early dry season fire was generally patchy, resulting in both large and small areas of burnt and unburnt vegetation. Furthermore, the patterns of burnt/unburnt patches differed with abundance of Sorghum (X^2 = 68.61; df =5, P < 0.001). In Sorghum plots, the patches of burnt ground tended to be large, but in plots with little or no Sorghum, there was a finer mosaic of smaller burnt patches (Figure 2). For example, in Sorghum plots, more than half the patches were ≥ 10 m in size (14% were ≥ 30 m) and only a third of burnt patches were < 3 m in size. In plots with little or no Sorghum almost all (99%) the burnt patches were < 10 m in size, 41% being less than 1 m in size (Figure 2).

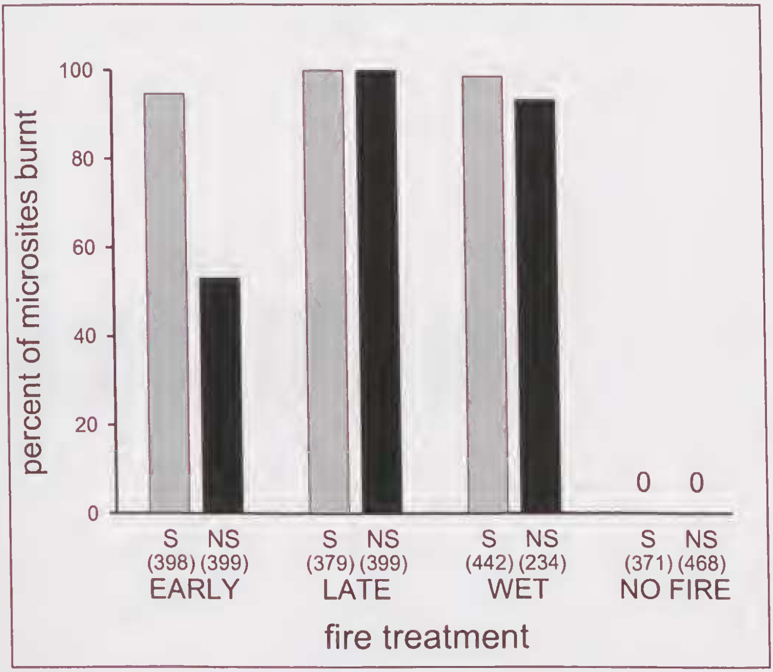

Figure 1. The percentage of total area (percentage of microsites at 10 cm each) burnt in each seasonal timing of fire treatment and Sorghum density. S = Sorghum plots; NS = plots with little or no Sorghum. Numbers refer to the total number of juvenile trees (< 200 cm height) in each study plot.

On a per hectare basis, the estimated area left unburnt in early dry season fire was 500 m^2 for Sorghum vs. 4,700 m^2 for plots with little or no Sorghum. Based on frequency distributions of patch size categories <0.5 m, 0.5-<3 m, 3-<10 m, 10-<20 m, 20-<30 m and >30 m (Figure 2), the estimated total area burnt per hectare in Sorghum plots was 10 m^2, 20 m^2, 240 m^2, 1,900 m^2, 2,860 m^2 and 4,470 m^2. By contrast, in plots with little or no Sorghum, the estimated total area burnt per hectare in the same patch size categories was 45 m^2, 475 m^2, 3,800 m^2, 970 m^2, 0 m^2 and 0 m^2, respectively.

The patchiness of late dry season fires was similar in Sorghum and little or no Sorghum plots, with essentially all ground burnt and all patch sizes ≥ 30 m. The wet season fire also created mainly large patches, nearly all being ≥ 30 m.

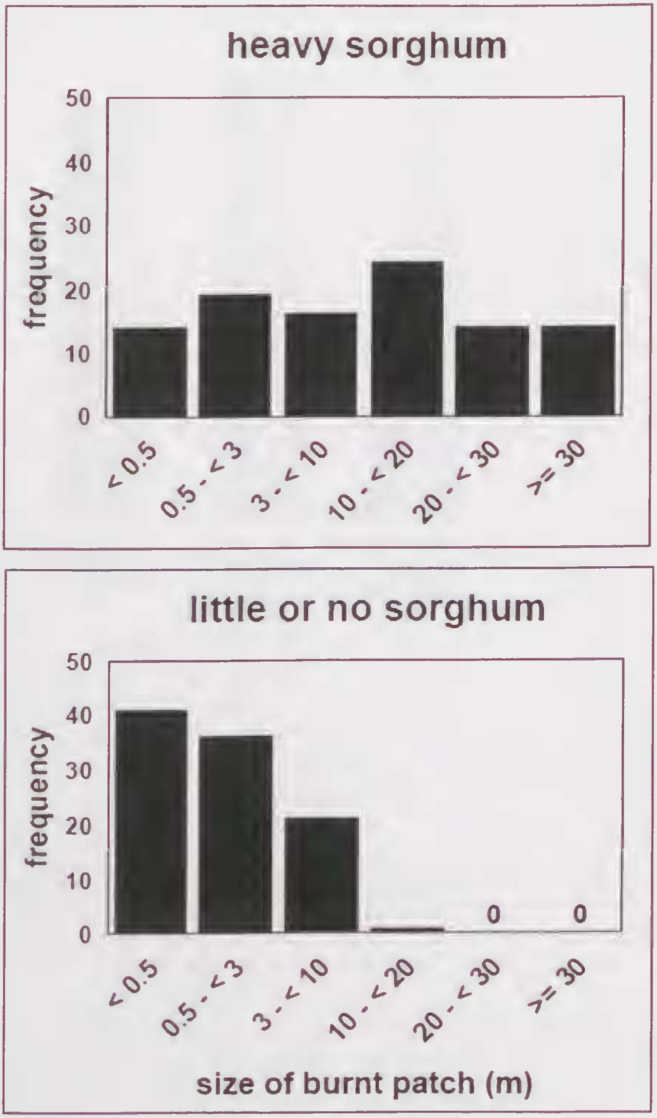

Figure 2. The frequency of burnt patches by size (linear distance (m) along transects), after early dry season fires in Sorghum plots and in plots with little or no Sorghum in the understorey.

Discussion

The fine-scale pattern of burns in early dry and late dry season fires is consistent with casual observations by field researchers and has not been documented previously in eucalypt savanna woodlands. In nearby sandstone heath vegetation, fine-scale patterns of patchiness relative to different fire regimes were examined by Price *et al* (2003), who reported 64% vs. 84% total area burnt in early dry season vs. late dry season fires, respectively, and with patch sizes generally < 10 m in both seasons. In sandstone country, unburnt patches were strongly associated with rockiness. However, in the absence of rocks, 100% of the area was burnt in late dry season fires (Price *et al.* 2003), yielding relative differences between fire seasons comparable to ours in the savanna woodlands.

Late dry season fires create a "scorched earth" with little probability that any juvenile tree would escape being burnt, regardless of abundance of Sorghum. Werner & Franklin (in press) report that 100% of juvenile trees (< 200 cm height) were burnt to the ground in the late dry season fire. These resprouted only from lignotubers but generally regained previous height the following year. Further, approximately 20% of saplings (200-500 cm height) were burnt to the ground but original height was not regained the following year (Werner & Franklin in press). Given the relatively slow average rates of height growth of small juvenile trees (Werner *et al.* 2006), it is very doubtful that many, if any, young trees would be able to grow out of the "fire trap" into a size large enough to withstand further fires, wherever late dry season fires occur more often than every 7-10 years.

By contrast, early dry season fire patterns differ with the type of understorey, and this can have different consequences for smaller juvenile trees. In Sorghum plots, where all microsites are burnt and the frequency distribution of patch sizes is relatively uniform, it is not surprising that nearly 100% of those juvenile trees that were < 100 cm height in these plots, and 50% or more of juveniles 100 to 200 cm height, suffered complete topkill and subsequently resprouted only from lignotubers (Werner & Franklin in press). High frequency of early dry season fires in Sorghum will not only enhance Sorghum abundance, but also greatly reduce the probability that juvenile trees will grow into the canopy. Alternatively, in areas with little or no Sorghum, where only about half the total area is burnt and where about half the burn patches are small (most likely reflecting lower flammability and or heterogeneity of the plant growth forms) only about 50% of those juvenile trees that were under 150 cm in height in these plots were topkilled and resprouted from lignotubers, and about 60% of young trees 150-500 cm height showed no first-year effects of early dry season fire (Werner & Franklin in press). This combination, early dry season fire and little or no Sorghum understorey, provides the highest probability that a young tree will avoid being burnt, and hence, the greatest chance it can eventually grow sufficient height to escape, and/or develop bark thick enough, to withstand subsequent fires, thus making the transition into the canopy.

The burn pattern for wet season fires shows at least one possible outcome, but we cannot say that it is most representative, as wet season fire behaviours would vary greatly from year to year depending on vagaries in the timing and amount of early rainfall events. The onset of the wet season can vary by some 10 weeks on the calendar (Taylor & Tulloch 1985). Our fires, set in December, were at the beginning of the wet season, and perhaps it is no surprise that results are similar to late dry season fires. More than 85% of juveniles suffered topkill with subsequent resprouting from lignotubers (Werner & Franklin in press).

The biological impact of wet season fires may be very different from that of late dry season fires for other reasons. For example, the smallest juvenile trees (< 100 cm height) are physiologically active during the wet season, but are generally leafless and dormant during late dry season fires, and any disturbance or removal of biomass may produce very different outcomes with respect to juvenile tree dormancy, survival and growth (Werner *et al.* 2006).

The differences in phenology between the two types of understorey, along with differences in total biomass and growth form that may carry fire differently, may help explain why fine-scale fire patterns are different between the two understorey types when burnt early in the dry season, but do not differ in late dry season or wet season fires. Annual Sorghum is among the earliest plants to complete its seasonal cycle, producing dry fuel prior to early dry season fires, whereas smaller annual grasses, perennial grasses and forbs remain green much longer, well into the middle or late dry season.

The degree to which grassy vs. non-grassy understoreys affect fine-scale burn patterns of fires set in different seasons remains unexplored in savannas across the world. Comparative information on burn patterns at a scale of juvenile trees could be important in developing a general understanding of bottlenecks in transitions between seeds or seedlings and canopy trees, which are a common feature on every other continent where this topic has been studied (Platt *et al.* 1988; Grace & Platt 1995; Chidumayo & Frost 1996; Scholes & Archer 1997; Gilliam & Platt 1999; Hoffmann 1999; Higgins *et al.* 2000; Bond & Midgley 2001; Midgley & Bond 2001; Hoffmann & Moreira 2002; Hoffmann & Solbrig 2003; Sankaran *et al.* 2004; Gardner 2006; Bond 2008; Hoffmann & Haridasan 2008; Hoffmann *et al.* 2009; Midgley *et al.* 2010). Specifically, comparisons of the role of the understorey in mitigating the fine-scale burn pattern of fires at different seasons in the mesic savannas of eastern and southern Africa could be very instructive. In contrast to the annual single-stemmed grasses of northern Australia, these African savannas are dominated by perennial tussock grasses (Bond & Van Wilgen 1996).

Implications for management

In northern Australia, early dry season fires are commonly lit by managers to reduce the probability of a late dry season fire occurring in the same year. I suggest that consideration be given to the understorey when setting these fires, since the presence of Sorghum greatly reduces the patchiness of ground-level burn and hence reduces the chance that individual juvenile trees will escape topkill, whereas lack of Sorghum yields a much patchier burn and hence increases the chance that young trees will avoid being burnt back. In sites where Sorghum is abundant, instead of the usual early dry season fire, the most appropriate action would be a wet season fire set soon after Sorghum seeds have germinated, which can eliminate Sorghum for several years (Press 1987; Lazarides *et al.* 1991; Cook *et al.* 1998; Miles 2003).

Unfortunately, some areas of northern Australia now have large stands of introduced African grasses (e.g. Gamba Grass) which brown off later in the dry season than does Sorghum, while increasing fuel loads up to seven times and thereby changing fire behaviour and potential impacts on biota (Rossiter *et al.* 2003; Setterfield *et al.* 2010). This has been the case in pine savannas of south-eastern North America where other introduced grasses flourish (Platt & Gottschalk 2001). It is not unreasonable to expect that tree regeneration will be greatly inhibited in those northern Australian savannas where African grasses have become established, as has been demonstrated in the cerrados of Brazil where an invasive grass inhibits tree regeneration (Hoffmann & Haridasan 2008).

Conclusion

From this study of fine-scale patchiness of fire in different seasons and Sorghum abundances, I suggest the following as a working hypothesis with respect to the transition of young trees to the canopy in the Australian savannas: under a regime of early dry season fires and with an understorey of native non-Sorghum species (excluding introduced grasses), a significant number of microsites or areas will escape being burnt, creating potential "windows of escape" for some juveniles which eventually grow to sapling and canopy sizes. Conversely, whenever repeat fires occur in other seasons and wherever the understorey is Sorghum, the probability of a juvenile tree growing into the canopy is extremely low.

Acknowledgements

The field work was initiated under a grant (Project SM22) from the Australian National Parks and Wildlife Service and under the auspices of the CSIRO, the land managers. Grateful acknowledgement and thanks goes to CSIRO technical staff I. D. Cowie, K. L. Tidemann, J. S. Cusack (dec.) and J. McCutcheon (dec.) for assistance in setting up the plots, and for recording species percentage ground cover and post-fire burn patterns; to CSIRO fire managers P. Brady and M. Gill and their crews for conducting the prescribed burns with great skill; to J. S. Cusack, I.D. Cowie and C. R. Dunlop (NT Herbarium) for species identification; to J. W. Shirley for figures; to M. J. Lawes and B. P. Murphy for valuable scientific reviews; and to L. Prior, D. Franklin and F. Douglas for constructive comments on the manuscript.

References

Andersen A.N., Braithwaite R.W., Cook G.D., Corbett L.C., Williams R.J., Douglas M., Gill A.M., Setterfield S. and Muller W.J. (1998) Fire research for conservation management in tropical savannas: introducing the Kapalga fire experiment. *Australian Journal of Ecology* 23, 95-110.

Andersen A.N., Cook, G.D. and Williams R.J. (eds) (2003) *Fire in Tropical Savannas: the Kapalga Experiment*. Springer, New York.

Andrew M.H. (1986) Population dynamics of the tropical annual grass *Sorghum intrans* in relation to local patchiness in its abundance. *Australian Journal of Ecology* 11, 209-217.

Andrew M.H. and Mott J.J. (1983) Annuals with transient seed banks: the population biology of indigenous *Sorghum* species of tropical north-west Australia. *Australian Journal of Ecology* 8, 265-276.

Bond W.J. (2008) What limits trees in C_4 grasslands and savanna? *Annual Review of Ecology, Evolution, and Systematics* 39, 641-659.

Bond W.J. and Midgley J.J. (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* 16, 15-51.

Bond W.J. and Van Wilgen B.W. (1996) *Fire and Plants*. Chapman & Hall, London.

Bowman D.M.J.S., Franklin D.C. and Price O.W. (2007) Land management affects grass biomass in the *Eucalyptus tetrodonta* savannas of monsoonal Australia. *Austral Ecology* 82, 446-452.

Chidumayo E.N. and Frost P. (1996). Population biology of miombo trees. In *The Miombo in Transition: Woodlands and Welfare in Africa* (ed B. Campbell), pp. 59-71. Centre for International Forestry Research (CIFOR), Bogor, Indonesia.

Cook G.D., Ronce O. and Williams R.J. (1998) Suppress thy neighbour: the paradox of a successful grass that is highly flammable, but harmed by fire. In *Proceedings of the 13th Conference on Fire and Forest* Meteorology (ed R. Webster), pp. 71-74. International Association of Wildland Fire, Lorne, Australia.

Finlayson C.M. and von Oertzen I. (eds) (1996) *Landscape and Vegetation Ecology of the Kakadu Region, Northern Australia*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Gardner T.A. (2006) Tree-grass coexistence in the Brazilian cerrado: demographic consequences of environmental instability. *Journal of Biogeography* 33, 448-463.

Gill A.M., Moore P.H.R. and Williams R.J. (1996). Fire weather in the wet-dry tropics of the World Heritage Kakadu National Park. *Australian Journal of Ecology* 21, 302-308.

Gill A.M., Pook E.W. and Moore P.H.R. (1987) *Measuring Fire Properties for Ecological Effects at Kakadu National Park*. Final report to the Australian National Parks and Wildlife Service, Canberra, Australia.

Gilliam F.S. and Platt W.J. (1999) Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. *Plant Ecology* 140, 15-26.

Grace S.L. and Platt W.J. (1995) Effects of adult tree density and fire on the demography of pregrass stage juvenile longleaf pine (*Pinus palustris* Mill.). *Journal of Ecology* 83, 75-86.

Higgins S.I., Bond W.J. and Trollope W.S.W. (2000). Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88, 213-229.

Hoffmann W.A. (1999) Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology* 80, 1354-1369.

Hoffmann W.A. and Haridasan M. (2008) The invasive grass, *Melinis minutiflora*, inhibits tree regeneration in a neotropical savanna. *Austral Ecology* 33, 29-36.

Hoffmann W.A.and Moreira A.G. (2002) The role of fire in population dynamics of woody plants. In *The Cerrados of Brazil* (eds P.S. Oliveira and R. J. Marquis), pp. 159-178. Columbia University Press, New York.

Hoffmann W.A. and Solbrig O.T. (2003) The roll of topkill in the differential response of savanna woody species to fire. *Forest Ecology and Management* 180, 273-286.

Hoffmann W.A., Adasme R., Haridasan M., de Carvalho M.T., Geiger E.L., Pereira M.A.B., Gotsch S.G. and Franco A.C. (2009) Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology* 90, 1326-1337.

Lazarides M., Hacker J. B. and Andrew M.H. (1991) Taxonomy, cytology and ecology of indigenous Australian Sorghums (*Sorghum* Moench: Andropogoneae: Poaceae). *Australian Systematic Botany* 4, 591-635.

Lehmann C.E.R., Prior L.D. and Bowman D.M.J.S. (2009) Fire controls population size structure in four dominant tree species in Australian mesic eucalyptus savanna. *Oecologia* 161, 505-515.

Lonsdale W.M. and Braithwaite R.W. (1991) Assessing the effects of fire on vegetation in tropical savannas. *Australian Journal of Ecology* 16, 363-374.

Midgley J J. and Bond W.J. (2001) A synthesis of the demography of African acacias. *Journal of Tropical Ecology* 17, 871-886.

Midgley J.J., Lawes M.J. and Chamaillé-Jammes, S. (2010) Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Australian Journal of Botany* 58, 1-11.

Miles G. (2003) Fire and spear grass: a case for wet-season burning in Kakadu. *Savanna Links* 25, 11.

Murphy B.P., Russell-Smith J. and Prior L.D. (2010) Frequent fires reduce tree growth in northern Australian savannas: implications for tree demography and carbon sequestration. *Global Change Biology* 16, 331-343.

Platt W. J. and Gottschalk R. M. (2001) Effects of exotic grasses on potential fine fuel loads in the groundcover of south Florida slash pine savannas. *International Journal of Wildland Fire* 10, 155-159.

Platt W.J., Evans G.W. and Rathbun S.L. (1988) The population dynamics of a long lived conifer (*Pinus palustris*). *American Naturalist* 131, 491-525.

Press A.J. (1987) Fire management in Kakadu National Park: the ecological basis for the active use of fire. *Search* 18, 244-248.

Press A.J., Lea D., Webb A. and Graham A. (1995) *Kakadu: Natural and Cultural Heritage and Management.* Australian Nature Conservation Agency and North Australian Research Unit of the Australian National University, Darwin, Australia.

Price O., Russell-Smith J. and Edwards A. (2003) Fine-scale patchiness of different fire intensities in sandstone heath vegetation in northern Australia. *International Journal of Wildland Fire* 12, 227-236.

Prior L.D., Brook B.W., Williams R.J., Werner P.A., Bradshaw C.J.A. and Bowman D.M.J.S. (2006) Environmental and allometric drivers of tree growth rates in a north Australian savanna. *Forest Ecology and Management* 234, 164-180.

Prior L.D., Williams R.J. and Bowman D.M.J.S. (2010) Experimental evidence that fire causes a tree recruitment bottleneck in an Australian tropical savanna. *Journal of Tropical Ecology* 26, 595-603.

Rossiter N.A., Setterfield S.A., Douglas M.M. and Hutley L.B. (2003) Testing the grass-fire cycle: exotic grass invasion in the tropical savannas of northern Australia. *Diversity and Distributions* 9, 169-176.

Russell-Smith J. and Edwards A.C. (2006) Seasonality and fire severity in savanna landscapes of monsoonal northern Australia. *International Journal of Wildland Fires* 15, 541-550.

Russell-Smith J., Ryan P.G. and Durieu R. (1997) A LANDSAT MSS-derived fire history of Kakadu National Park, monsoonal Australia, 1980-94: seasonal effect, frequency and patchiness. *Journal of Applied Ecology* 34, 748-766.

Russell-Smith J., Whitehead P.J., Cook G.D. and Hoare J.L. (2003*a*) Response of eucalyptus-dominated savanna to frequent fires: lessons from Munmarlary, 1973-1996. *Ecological Monographs* 73, 349-375.

Russell-Smith J., Yates C., Edwards A., Allan G.E., Cook G.D., Cooke P., Craig R., Heath B. and Smith R. (2003*b*) Contemporary fire regimes of northern Australia, 1997-2001. *International Journal of Wildland Fire* 12, 283-297.

Sankaran M., Ratnam J. and Hanan N.P. (2004) Tree-grass coexistence in savannas revisited—insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* 7, 480-490.

Scholes R.J. and Archer S.R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28, 517-544.

Setterfield S.A., Rossiter-Rachor N.A., Hutley L.B., Douglas M.M. and Williams R.J. (2010) Turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behaviour in northern Australia savannas. *Diversity and Distributions* 16, 854-861.

Spangler R.E. (2003) Taxonomy of *Sarga*, *Sorghum* and *Vacoparis* (Poaceae: Andropogoneae). *Australian Systematic Botany* 16, 279-299.

Taylor J.A. and Dunlop C.R. (1985) Plant communities of the wet-dry tropics of Australia: the Alligator Rivers region, Northern Territory. *Proceedings of the Ecological Society of Australia* 13, 83-127.

Taylor J.A. and Tulloch D. (1985) Rainfall in the wet-dry tropics: extreme events at Darwin and similarities between years during the period 1870-1983 inclusive. *Australian Journal of Ecology* 10, 281-295.

Werner P.A. (1986) *Population Dynamics and Productivity of Selected Forest Trees in Kakadu National Park.* Final report to the Australian National Parks and Wildlife Service, Canberra, Australia.

Werner P.A. (2005) Impact of feral water buffalo and fire on growth and survival of mature savanna trees: An experimental field study in Kakadu National Park, northern Australia. *Austral Ecology* 30, 625-647.

Werner P.A. and Franklin D.C. (in press) Resprouting and mortality of juvenile eucalypts in an Australian savanna: Impacts of fire season and annual sorghum. *Australian Journal of Botany*

Werner P.A., Cowie I.D. and Cusack J.S. (2006) Juvenile tree growth and demography in response to feral water buffalo in savannas of northern Australia: an experimental field study in Kakadu National Park. *Australian Journal of Botany* 54, 283-296.

Williams P.R. (2009) Contrasting demographics of tropical savanna and temperate forest eucalypts provide insight into how savannas and forests function: a case study using *Corymbia clarksoniana* from north-eastern Australia. *Austral Ecology* 34, 120-131.

Williams R.J., Cook G.D., Gill A.M. and Moore P.H.R. (1999) Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* 24, 50-59.

Williams R.J., Gill A.M. and Moore P.H.R. (1998) Seasonal changes in fire behaviour in a tropical savanna in northern Australia. *International Journal of Wildland Fire* 8, 227-239.

Williams R.J., Müller W.J., Wahren C.H., Setterfield S.A. and Cusack J. (2003) Vegetation. In *Fire in Tropical Savannas: The Kapalga Experiment* (eds A.N. Andersen, G.D. Cook and R. J. Williams), pp. 79-106. Springer, New York.